



Chimpanzee and human midfoot motion during bipedal walking and the evolution of the longitudinal arch of the foot



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ABSTRACT

The longitudinal arch of the human foot is commonly thought to reduce midfoot joint motion to convert the foot into a rigid lever during push off in bipedal walking. In contrast, African apes have been observed to exhibit midfoot dorsiflexion following heel lift during terrestrial locomotion, presumably due to their possession of highly mobile midfoot joints. This assumed dichotomy between human and African ape midfoot mobility has recently been questioned based on indirect assessments of *in vivo* midfoot motion, such as plantar pressure and cadaver studies; however, direct quantitative analyses of African ape midfoot kinematics during locomotion remain scarce. Here, we used high-speed motion capture to measure three-dimensional foot kinematics in two male chimpanzees and five male humans walking bipedally at similar dimensionless speeds. We analyzed 10 steps per chimpanzee subject and five steps per human subject, and compared ranges of midfoot motion between species over stance phase, as well as within double- and single-limb support periods. Contrary to expectations, humans used a greater average range of midfoot motion than chimpanzees over the full duration of stance. This difference was driven by humans' dramatic plantarflexion and adduction of the midfoot joints during the second double-limb support period, which likely helps the foot generate power during push off. However, chimpanzees did use slightly but significantly more midfoot dorsiflexion than humans in the single limb-support period, during which heel lift begins. These results indicate that both stiffness and mobility are important to longitudinal arch function, and that the human foot evolved to utilize both during push off in bipedal walking. Thus, the presence of human-like midfoot joint morphology in fossil hominins should not be taken as indicating foot rigidity, but may signify the evolution of pedal anatomy conferring enhanced push off mechanics.

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1. Introduction

The human foot is distinguished from the feet of all other primates by the presence of a longitudinal arch, which is architecturally defined by the relative orientations of the tarsal and metatarsal bones and spans numerous joints of the midfoot region, including the tarsometatarsal and transverse tarsal joints. This structure is thought to be a critical adaptation for bipedal locomotion, in part because it is absent from the feet of our closest living relatives, the African apes. Whereas the mobile midfoot joints of African apes are believed to enhance pedal grasping on arboreal

supports (Elftman and Manter, 1935a; Susman, 1983; DeSilva, 2010), the human longitudinal arch is believed to stiffen the midfoot region by reducing motion at these joints, thereby providing a stable push off lever during bipedal walking (Elftman and Manter, 1935b; Bojsen-Møller, 1979). This functional distinction is based largely on qualitative observations of between-species differences in midfoot motion during push off, which begins when the heel is first lifted from the ground and ends when the toes lose contact. While the human foot appears to remain rigid following heel lift, the African ape foot dorsiflexes slightly about the midfoot joints (Elftman and Manter, 1935a; D'Août et al., 2002; Vereecke et al., 2003; DeSilva, 2010), a motion that has been named the 'midtarsal break' (Susman, 1983).

A number of soft and hard tissue features in the foot are thought to be responsible for the observed differences in human and African

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ape midfoot mobility. Humans possess a thick plantar aponeurosis that tenses when the metatarsophalangeal joints are dorsiflexed during push off, elevating the longitudinal arch and stiffening the midfoot with the help of the intrinsic foot muscles (Hicks, 1954; Caravaggi et al., 2010; Kelly et al., 2015). African apes are thought to lack this mechanism because they possess less developed plantar aponeuroses (Susman, 1983), and also do not display the joint articular surface features present in humans that are believed to passively constrain midfoot motion. These include morphology that provides a 'locking' mechanism between the calcaneus and cuboid (Bojsen-Møller, 1979) and a flat rather than rounded (concavo-convex) cuboid-metatarsal joint (DeSilva, 2010; Proctor, 2013). The presence or absence of these features has often been used to make inferences about midfoot structure and function in fossil hominins. Some have interpreted hominin foot bones presenting more African ape-like joint surface morphology as indicating the retention of arboreal adaptations (Sarmiento and Marcus, 2000; Zipfel et al., 2011), and those presenting more human-like morphology as indicating a reduced reliance on climbing in favor of more proficient bipedalism (Langdon et al., 1991; DeSilva, 2010; Ward et al., 2011; Harcourt-Smith et al., 2015). Thus, the assumed dichotomy in midfoot mobility in humans and African apes has played a pivotal role in debates concerning the evolution of bipedalism, as well as in defining the adaptive significance of the human longitudinal arch.

This dichotomy has recently come under scrutiny from several studies that have investigated midfoot function empirically. Three-dimensional (3D) motion capture studies of human walking, including one using bone pin-mounted markers (Lundgren et al., 2008), have revealed high ranges of motion in the joints of the longitudinal arch during the stance phase of a stride (e.g., Carson et al., 2001; Leardini et al., 2007; Rankine et al., 2008). In addition, using pressure-sensing technology, researchers have discovered that some humans exhibit midfoot pressure peaks that resemble those produced by non-human great apes during the midtarsal break (Crompton et al., 2012; Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015). Finally, Greiner and Ball (2014) demonstrated that cadaveric human and chimpanzee feet possess similar passive ranges of motion at the midfoot joints, whereas the feet of macaques and baboons are more mobile. The results of these studies potentially contradict previous notions about relative foot mobility in humans and African apes, and call into question the validity of using osteological features as indicators of midfoot joint range of motion (Bates et al., 2013; Greiner and Ball, 2014). They also challenge the frequent conflation of midfoot joint 'mobility' with midfoot joint 'stiffness' and/or 'compliance;' whereas 'mobility' can be thought of as absolute range of motion allowed at the midfoot joints, joint 'stiffness,' following a mechanical definition, is the amount of torque about a joint relative to the motion that occurs, and 'compliance' is the inverse of 'stiffness.' These studies undermine the assumed relationship between these variables in hominoids by hinting at the possibility that humans possess midfoot joints that are relatively mobile, but also capable of stiffening the foot during walking (Lundgren et al., 2008; Bates et al., 2013; Greiner and Ball, 2014).

Currently, our understanding of hominoid midfoot function is limited by a lack of quantitative foot kinematic data from African apes during locomotion. Previous studies have focused primarily on a small interval of stance, the beginning of heel lift, and have provided almost exclusively qualitative descriptions of differences between humans and African apes (Elftman and Manter, 1935a; Susman, 1983; D'Août et al., 2002). DeSilva (2010) reported the first quantitative measures of midtarsal break magnitudes in humans and African apes, but he relied on two-dimensional lateral view images and only measured midfoot angles at heel lift. Recent

human walking studies have used 3D kinematics to reveal important motion patterns in the midfoot outside of the sagittal plane, and particularly at the beginning and end of stance phase, when one foot is pushing off the ground while the other is beginning to accommodate weight (e.g., Leardini et al., 2007; Rankine et al., 2008). This double limb-support period is critical to the mechanical cost of human bipedal walking (Donelan et al., 2002; Umberger, 2010), but does not coincide with the timing of the midtarsal break in African apes, which occurs just after midstance (Elftman and Manter, 1935a; Susman, 1983). Thus, we must investigate periods of stance other than heel lift in these animals.

To improve our understanding of hominoid midfoot motion we collected marker-based 3D kinematic data from humans and chimpanzees during bipedal walking. Chimpanzees are our closest living relatives and are contrasted with humans in virtually all analyses of early hominin foot morphology, making an understanding of their foot biomechanics an important comparative context for human evolutionary studies. Further, by investigating bipedalism in both species, we can rule out differences in kinematics that could be due to chimpanzees' use of quadrupedal gaits, as well as maximize the applicability of our findings to reconstructions of fossil hominin locomotion. We tested the hypothesis that the human longitudinal arch and its associated soft and hard tissue structures reduce midfoot motion across a bipedal walking step, and during push off in particular. In keeping with previous observations of chimpanzee locomotion, we predicted that chimpanzees would use a greater range of motion in the midfoot region in the sagittal plane than humans due to the dorsiflexion that occurs during the midtarsal break. We also anticipated a greater range of motion in the chimpanzee midfoot outside of the sagittal plane, as previous investigations have suggested the potential for high coronal plane mobility in the chimpanzee transverse tarsal joint complex (Lewis, 1980; Rose, 1986; Thompson et al., 2014).

2. Methods

2.1. Data collection

We collected 3D kinematic data from five male humans (28 ± 1 yrs, 68 ± 6 kg) and two male chimpanzees (7.7 ± 0.7 yrs, 42 ± 7 kg). All human subjects reported no recent foot pain and were determined to have 'normal' longitudinal arches based on arch height indices (0.35 ± 0.01 mean) within one standard deviation of the mean reported for a large sample of adult males (0.34 ± 0.03 mean; Butler et al., 2008). Chimpanzees were housed at a facility accredited by the Association for Assessment and Accreditation of Animal Laboratory Care International, and all experimental procedures involving chimpanzees were approved by Stony Brook University's Institutional Animal Care and Use Committee. All experimental procedures involving humans were approved by Stony Brook University's Institutional Review Board, and human subjects provided informed written consent before participating in experimental procedures.

During experiments, subjects were video recorded at 150 Hz using a four-camera motion capture system (Xcitex Inc., Woburn, MA) while walking on a flat 11 m runway at self-selected speeds. Chimpanzee subjects had been trained to walk bipedally and had roughly two years of experience doing so prior to the start of data collection. During experiments, they were encouraged to walk bipedally by an animal trainer who offered food rewards and positive reinforcement. From the video recordings, we selected 10 representative steps per chimpanzee subject and five steps per human subject for analysis. In all selected steps, subjects walked straight forward on the runway without any noticeable change in

speed. Chimpanzee subjects walked with abducted halluces and extended digits, which was typical for these individuals.

2.2. Three-dimensional kinematics

We designed our methodology for calculating 3D joint motion following the guidelines provided in Hamill and Selbie (2004). Before video recording, we applied markers by drawing 1 cm circles on the legs and feet of our subjects using non-toxic paint. Although the use of surface markers can lead to error in kinematics calculations due to motion of soft tissue relative to the underlying bone, markers placed on the foot are less susceptible to such errors than those placed on other parts of the lower limb due to the lack of significant intervening tissue between skin and bone (Leardini et al., 2005). Furthermore, the motion of surface markers relative to bone in the human foot is reported to be typically less than 4 mm (Maslen and Ackland, 1994; Tranberg and Karlsson, 1998). Nevertheless, to minimize such errors we selected marker locations away from regions of substantial subcutaneous soft tissue that could cause extraneous motion. Marker locations were determined by palpable bony landmarks or by measuring discrete distances from palpable bony landmarks (Table 1, Fig. 1). In humans, we identified landmarks following standard clinical techniques (Tixa, 2003), and in chimpanzees, we identified landmarks by referring to x-rays of the subjects' feet.

We defined 'rearfoot' and 'forefoot' segments by placing three markers on the skin overlying the calcaneus (rearfoot) and four markers on the skin overlying metatarsals 2–5 (forefoot). Placing three or more non-collinear markers on a segment allows one to define a 3D local coordinate system for that segment. A 'neutral position' is then used to align the local coordinate system with the global coordinate system of the laboratory. For each experimental session from which subject data were used, we defined neutral position as a single instant from the recorded video of a walking step where the leg and foot were configured to meet the following criteria: the long axis of the foot was oriented in the direction of travel, the leg was perpendicular to the ground, and the plantar surface of the foot was flat against the substrate with the digits extended (Fig. 2). For all experimental sessions, the neutral position that we used was taken from a single step at a moment prior to midstance. The purpose of defining a neutral position is to calculate a rotation matrix that aligns the segment's local coordinate system axes with those of the laboratory's global coordinate system. This rotation matrix is then used to determine the segment's instantaneous orientation relative to the global coordinate system in locomotion trials. Subsequently, the local coordinate systems of adjacent segments can be used to calculate 3D motion between the segments. Their orientations relative to one another in the neutral position are set at 0° in all three anatomical planes. In locomotion trials, motion between segments is calculated as the rotations in each anatomical plane that

are necessary to restore the relative segment orientations from the neutral position.

Because we divided the foot into rearfoot and forefoot segments, our method allowed us to calculate the cumulative joint motion between these segments, which should occur largely at the transverse tarsal joint complex (i.e., calcaneocuboid and talonavicular joints) and at the tarsometatarsal joints of pedal rays 2 to 5 (Lundgren et al., 2008; DeSilva, 2010; Greiner and Ball, 2014). Hereafter, we refer to motion between the rearfoot and forefoot segments as 'midfoot motion.' This approach is taken in many human 3D kinematics studies (e.g., Kidder et al., 1996; Carson et al., 2001; Hunt and Smith, 2004) because 3D motion cannot be accurately resolved at individual midfoot joints without the use of bone pins or fluoroscopic imaging (e.g., Nester et al., 2007).

2.3. Data analysis

Three-dimensional marker coordinate data from the selected steps were extracted using ProAnalyst (Xcitex, Inc.) and imported into MATLAB (The Mathworks Inc., Natick, MA), where they were filtered using a fourth order low pass Butterworth filter with 5, 7, and 6 Hz cutoff frequencies for the X, Y, and Z coordinates, respectively. Cutoff frequencies were calculated by performing an analysis of the root mean square of the residuals of filtered versus unfiltered data from five random steps, and determining which cutoff frequency maximized the removal of signal noise in the motion capture system while minimizing distortion of the true signal, as described by Winter (2005). We calculated 3D joint angles from the coordinate data using a custom-modified version of the KineMat MATLAB package (Reinschmidt and van den Bogert, 1997). This package applies a singular value decomposition algorithm to minimize residuals in marker position calculations due to soft tissue motion (Söderkvist and Wedin, 1993), which reduces errors in angle calculation due to violation of the rigid body assumption of no within-segment movement. Following International Society of Biomechanics recommendations (Wu et al., 2002), we calculated angles using the Joint Coordinate System method with a ZYX Cardan rotation sequence (Grood and Suntay, 1983). This method calculates angles as rotation of the distal segment relative to the proximal segment about three axes: the mediolateral axis of the proximal segment (rearfoot), the vertical axis of the distal segment (forefoot), and a floating axis that is orthogonal to both of these. These rotations represent motion in the sagittal plane (plantar-flexion-dorsiflexion), transverse plane (abduction-adduction), and coronal plane (inversion-eversion), respectively (Fig. 3).

We calculated the instantaneous angles between the rearfoot and forefoot segments throughout the full duration of stance phase, which was defined as beginning when the foot contacted the substrate (touchdown) and ending when the hallux lost contact with the substrate (liftoff) based on visual assessment from the video recordings (Fig. 4). We subdivided stance phase into three support periods as in O'Neill et al (2015; see Fig. 4 for period definitions): first double-limb support (DS1), single-limb support (SS), and second double-limb support (DS2). For each step, we calculated the total range of motion throughout stance and within each support period for each anatomical plane. Within species, steps were used as individual data points and pooled across subjects (chimpanzees, $n = 20$; humans, $n = 25$). We used Wilcoxon Rank–Sum tests to test for differences in range of motion between species in each plane and each support period, and we used a Bonferroni correction for multiple comparisons to adjust the alpha value in significance testing ($\alpha = 0.004$). All statistical tests were performed using R 3.2.1 (R Development Core Team, 2014).

Table 1
Marker locations used to measure motion between rearfoot and forefoot segments in human and chimpanzee subjects (see Fig. 1).

Segment	Marker location
Rearfoot	Peroneal trochlea
	3 cm posterior to peroneal trochlea
	1.5 cm posterior and 2 cm inferior to peroneal trochlea
Forefoot	Metatarsal 2 head
	Metatarsal 2 base
	Metatarsal 4 head
	Metatarsal 5 base

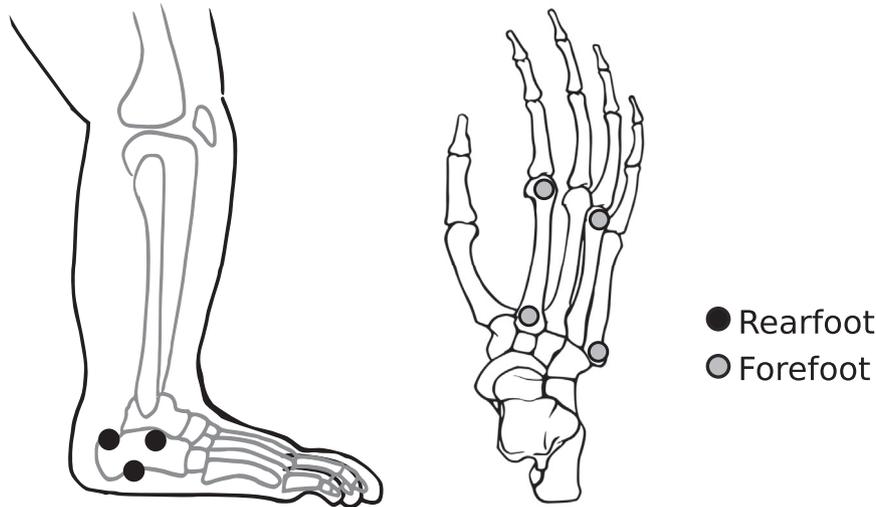


Figure 1. Marker locations used to define segments of the foot (see Table 1). Chimpanzee foot skeleton superior view redrawn from Morton (1922).

2.4. Speed estimation

To accurately track marker position and quantify 3D foot kinematics, we used zoomed-in camera views that provided close-cropped video of the foot and leg, but precluded the measurement of whole stride speed of progression and duty factor. However, we did calculate stance phase duration, which is tightly correlated with duty factor and should therefore give an indication of relative speed (Demes et al., 1994; Vereecke et al., 2004). To estimate speed, we used subject-specific linear regression equations that we developed in separate experiments with zoomed-out camera views that showed the whole body and allowed us to measure motion of the pelvis across a full stride. In these experiments, we determined the relationship between stance phase duration during bipedal walking and Froude number, which is a measure of dimensionless velocity that assumes dynamic similarity between individuals (Alexander and Jayes, 1983). The Supplementary Online Material (SOM) contains a more detailed description of speed estimation methods.

3. Results

For the steps included in our analysis we estimated the same average Froude number for both species (0.21 ± 0.04 for

chimpanzees, 0.21 ± 0.02 for humans; SOM Table S1). In chimpanzee steps, the double-limb support periods (DS1 and DS2) took up the first and last $25 \pm 4\%$ of stance on average, whereas in human steps they took up the first and last $18 \pm 2\%$ (Fig. 4), similar to an earlier study of humans and bipedal chimpanzees walking at matched dimensionless speeds (O'Neill et al., 2015). Three-dimensional kinematic results where all steps have been averaged within species are depicted in Figure 5 and presented in Table 2. Three-dimensional kinematic results for individual subjects are depicted in SOM Figure 1 and reveal that within species, patterns and magnitudes of motion are very similar among subjects. Supplementary videos present steps from both chimpanzee subjects (SOM Videos 1 and 2) and one human subject (SOM Video 3).

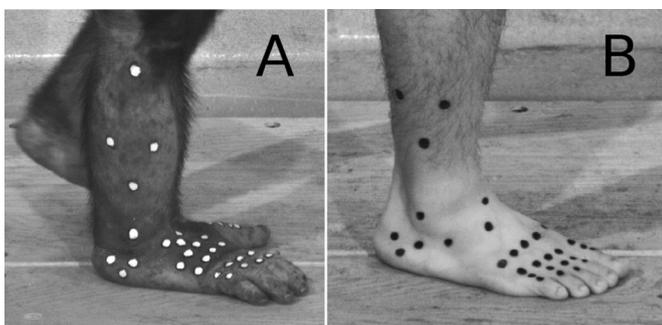


Figure 2. Examples of neutral positions used to calculate 3D kinematics for chimpanzee (A) and human (B) subjects. Neutral position is defined as the long axis of the foot oriented in the direction of travel, the leg perpendicular to the ground, and the plantar surface of the foot flat against the substrate with the digits extended.

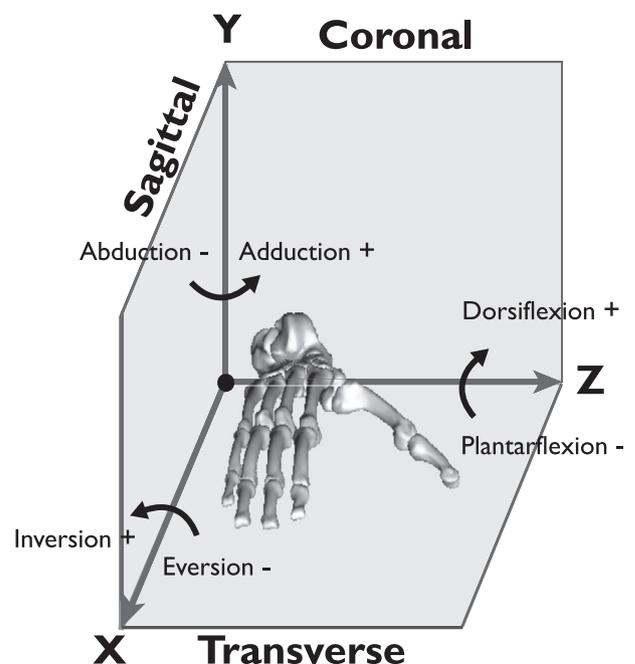


Figure 3. Planes of motion relative to the foot and signs of motions in each plane.

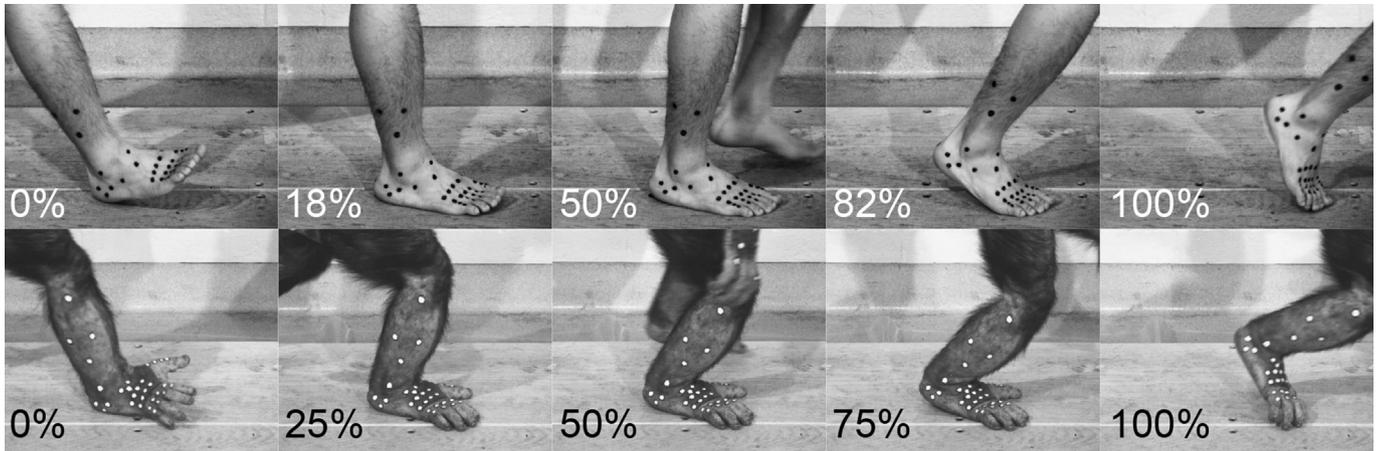


Figure 4. The stance phase of a bipedal walking stride begins at touchdown (0%), continues through midstance (50%), and ends at liftoff of the same foot (100%). Stance phase is divided among the first double-limb support (DS1; human: 0–18%, chimpanzee: 0–25%), single-limb support (SS; human: 18–82%, chimpanzee: 25–75%), and the second double-limb support periods (DS2; human: 82–100%, chimpanzee: 75–100%). DS1 = touchdown of the ipsilateral foot to liftoff of the contralateral foot, SS = liftoff to touchdown of the contralateral foot, DS2 = touchdown of the contralateral foot to liftoff of the ipsilateral foot.

Supplementary online video related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2016.12.002>.

Humans used significantly greater ranges of sagittal plane midfoot motion across the full stance phase than chimpanzees (Fig. 5A–C; Table 2). Among the support periods, humans used a significantly greater range of motion than chimpanzees during DS2, whereas chimpanzees used a significantly greater range of motion during SS. Humans rapidly dorsiflexed their midfoot joints during DS1, exhibited little motion during SS, then dramatically plantarflexed them during DS2 (Fig. 5B; SOM Fig. 1D). In contrast,

chimpanzees slightly plantarflexed their joints following touchdown, steadily dorsiflexed them across SS, and then plantarflexed them, but to a much lesser degree than humans, during DS2 (Fig. 5A; SOM Fig. 1A).

Midfoot coronal plane patterns and ranges of motion were similar in both species across stance (Fig. 5D–F; $p = 0.9$; see also SOM Fig. 1B, E), exhibiting gradual eversion across the first half of stance, followed by more rapid inversion prior to liftoff. However, humans used significantly more motion than chimpanzees during SS (Table 2).

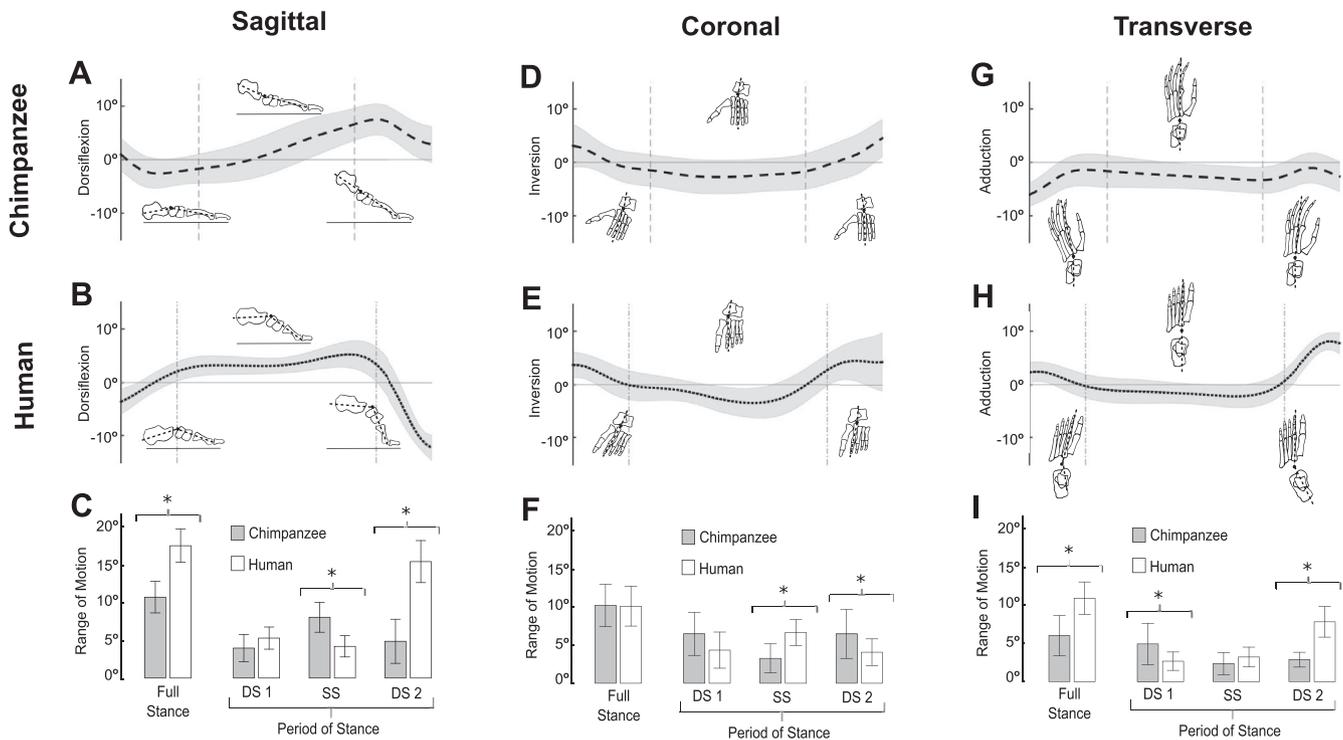


Figure 5. Average motion (black dotted/dashed lines, \pm s.d. in gray shading) between the rearfoot and forefoot segments across stance phase in the sagittal (A, B; dorsiflexion+/plantarflexion–), coronal (D, E; inversion+/eversion–), and transverse (G, H; adduction+/abduction–) planes (see Fig. 3). Vertical dashed lines indicate the beginning and end of single-limb support periods (see Fig. 4 for definitions of support periods). Ranges of motion depicted in foot illustrations are exaggerated to clarify motion and are schematic representations of what foot motion would look like if restricted to a single plane. C, F, I) Average range of motion over full stance, first double-limb support (DS1), single-limb support (SS), and second double-limb support (DS2). Stars indicate significant differences between species.

Table 2
Average range of motion between rearfoot and forefoot segments during stance in humans and chimpanzees.

Plane	Period ^a	Chimpanzee	Human	<i>p</i> -Value ^b	<i>W</i> _{20,25} ^c
Sagittal	DS1	4.1 ± 1.9°	5.4 ± 1.5°	0.010	354
	SS	8.3 ± 2.0°	4.3 ± 1.4°	<0.001	474
	DS2	5.0 ± 3.0°	15.8 ± 2.9°	<0.001	499
	Full stance	11.0 ± 2.1°	18.0 ± 2.3°	<0.001	493
Coronal	DS1	6.5 ± 2.8°	4.3 ± 2.4°	0.009	363
	SS	3.3 ± 1.9°	6.6 ± 1.7°	<0.001	456
	DS2	6.5 ± 3.2°	4.1 ± 1.7°	0.006	368
Transverse	Full stance	10.2 ± 2.8°	10.1 ± 2.6°	0.900	260
	DS1	5.0 ± 2.7°	2.7 ± 1.2°	0.003	379
	SS	2.4 ± 1.5°	3.2 ± 1.3°	0.030	345
	DS2	2.9 ± 1.0°	7.9 ± 2.0°	<0.001	494
	Full stance	6.0 ± 2.6°	11.0 ± 2.1°	<0.001	455

^a DS1 = first double-limb support period (human: 0–18%, chimpanzee: 0–25%), SS = single-limb support period (human: 18–82%, chimpanzee: 25–75%), DS2 = second double-limb support period (human: 82–100%, chimpanzee: 75–100%).

^b Results of Wilcoxon Rank–Sum tests. Bold font indicates significant difference after applying a Bonferroni correction to the alpha value (alpha = 0.004).

^c Wilcoxon rank-sum test statistic, where subscript denotes $n_1 = 20$ chimpanzee steps and $n_2 = 25$ human steps. For reference, $W_{20,25} = 372$ corresponds to $p = 0.005$ (Zar, 1984).

Humans used significantly greater ranges of motion in the transverse plane across stance than chimpanzees (Fig. 5G–I, Table 2; see also SOM Fig. 1C,F). This difference was driven largely by humans' dramatic adduction of the forefoot during DS2, which was significantly greater in magnitude than a similar motion in chimpanzees during this period. Chimpanzees did, however, use significantly more transverse plane motion than humans during DS1; during this period, chimpanzees touched down with abducted joints that they subsequently adducted, whereas humans slightly abducted their joints from near neutral position at touchdown.

4. Discussion

4.1. Midfoot kinematics during bipedal walking

The human longitudinal arch is thought to have evolved to stiffen the foot during bipedal walking (Elftman and Manter, 1935a, b; Bojsen-Møller, 1979; Susman, 1983; DeSilva, 2010), and therefore we predicted that chimpanzees would use a greater range of midfoot motion when walking bipedally than humans, and in particular during push off. Contrary to the first part of this prediction, we found that humans actually use a significantly greater total range of motion across the midfoot joints than chimpanzees over the full duration of stance phase. The critical differences between species driving this surprising result become apparent when dividing stance into double- and single-limb support periods. During DS2, humans dramatically plantarflex and adduct the midfoot joints, which corresponds to elevation of the longitudinal arch at the end of push off. This motion is likely driven largely by passive dorsiflexion of the metatarsophalangeal joints that tenses the plantar aponeurosis (Hicks, 1954; Erdemir et al., 2004; Caravaggi et al., 2009) and is augmented by activation of the intrinsic foot muscles (Caravaggi et al., 2010; Kelly et al., 2014, 2015). We suggest two roles that this motion may play in human walking. First, plantarflexion of the forefoot relative to the rearfoot coincides roughly with the timing of a spike in ankle joint power that occurs during DS2 as the foot is pushing off from the ground (e.g., Winter et al., 1996). Inverse dynamics studies have revealed that this midfoot motion generates positive power that complements the power produced at the ankle (MacWilliams et al., 2003; Bruening et al., 2012; Dixon et al., 2012), and we suggest that it may

therefore contribute to raising and/or accelerating the center of mass at the end of stance phase. Second, adduction at the midfoot joints allows the forefoot to stay planted while the lower limb is externally rotating at the end of stance. Midfoot adduction thereby helps to keep the center of pressure under the foot's first and second rays during DS2. This allows humans to push off from the part of the forefoot that is furthest from the ankle joint axis of rotation (Bojsen-Møller, 1979), providing the longest possible out-lever arm for the triceps surae muscles during their period of maximal power production in a walk (e.g., Farris and Sawicki, 2012).

Although the human midfoot exhibits greater mobility overall than that of chimpanzees during bipedal walking, chimpanzees do use a significantly greater amount of sagittal plane motion during SS. Because heel lift begins in this period, the steady midfoot dorsiflexion exhibited by our subjects is consistent with expectations that chimpanzees briefly raise their heels from the ground while the forefoot remains in contact during the midtarsal break (Elftman and Manter, 1935a; Susman, 1983). Humans, on the other hand, display little midfoot dorsiflexion during SS, and if we assume similar midfoot torques in both species following heel lift, these results suggest that human feet are stiffer than those of chimpanzees. However, midfoot torques could differ between species based on relative magnitude and orientation of ground reaction forces, as well as center of pressure position, none of which were quantified in this study. Thus, more data on joint mechanics during locomotion are necessary before we can definitively conclude that humans possess stiffer feet than chimpanzees, although the kinematic data from this study support the idea.

These results highlight an interesting paradox concerning human midfoot joint function: although the human foot indeed appears capable of resisting dorsiflexion torques, the midfoot joints retain considerable mobility that is used during push off. Chimpanzees, on the other hand, possess feet that seem less able to resist dorsiflexion during heel lift than the feet of humans, and thus we do not fully refute our prediction that humans have less mobile feet than chimpanzees during push off. Nevertheless, the amount of dorsiflexion allowed at the chimpanzee midfoot joints during SS is only 4° greater than that allowed in humans on average (Table 2), suggesting that the absolute difference in midfoot motion following heel lift between humans and chimpanzees is not as great as often stated. Although directly comparable data from other primates are lacking, descriptions and measurements of foot motion in Old World monkeys and gibbons indicate that these species exhibit midtarsal breaks that far exceed those of chimpanzees, and that they therefore possess considerably more mobile feet (Meldrum, 1991; Vereecke and Aerts, 2008; Berillon et al., 2010; DeSilva, 2010; Hirasaki et al., 2010).

Our results reveal that chimpanzees also use a significantly greater range of motion than humans in the transverse plane during DS1, but a significantly smaller range of coronal plane motion during SS, although the average magnitude of difference between species in both instances is only about 3°. Chimpanzees touch down with a relatively abducted forefoot, which they subsequently adduct during DS1. The purpose of this motion is currently unclear, but could be related to chimpanzees' preferred foot posture at touchdown, where the whole foot is considerably inverted relative to the leg such that the lateral side makes first contact with the ground (Fig. 4; Elftman and Manter, 1935a; Susman, 1983; Vereecke et al., 2003). In the coronal plane, the greater range of motion used by humans during SS is driven largely by between-species differences in the timing of the beginning and end of the period, rather than a different motion pattern (Fig. 5D, E), and thus is unlikely to be of functional significance. The similarity in pattern and magnitude of coronal plane motion across stance between humans and chimpanzees runs counter to our prediction of high mobility in the

latter, which was based on functional interpretations of transverse tarsal joint complex articular surface morphology (Lewis, 1980; Rose, 1986) and passive range of motion measurements (Thompson et al., 2014).

Our finding that chimpanzees walk bipedally with less midfoot joint mobility than humans overall is consistent with several recent empirical investigations of hominoid midfoot function, which found surprising overlap among humans and *Pan* species in passive joint mobility and plantar pressure distributions (Bates et al., 2013; Greiner and Ball, 2014). These studies concluded that soft tissue structures, not joint morphology, are primarily responsible for stiffening the human midfoot following heel lift. If the normal functions of these structures are impaired due to any number of factors (e.g., ligamentous laxity, muscle weakness), then an African ape-like break is possible (Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015). These findings have important implications for the interpretation of midfoot joint morphology in fossil hominins. Human-like morphologies do not necessarily signify a loss of midfoot mobility, as some have argued (Langdon et al., 1991; DeSilva, 2010; Ward et al., 2011; Proctor, 2013; Prang, 2016a). However, they may reflect an adaptation for greater foot stiffness and power generation during push off in bipedal walking.

The midfoot joint angles measured from humans in this study closely agree with those reported in other human 3D foot kinematic studies that divide the foot into rearfoot and forefoot segments (e.g., Carson et al., 2001; Leardini et al., 2007; Portinaro et al., 2014). This correspondence gives us confidence that not only are the human results from this study robust, but that our results provide an accurate representation of chimpanzee midfoot motion during bipedal walking as well. Our human subject results also show broad agreement with the lone study that used bone pin-mounted markers to precisely quantify midfoot joint motion (Lundgren et al., 2008), providing further support for the robustness of our data. Importantly, the large plantarflexion and adduction motions that we measured at the human midfoot joints during DS2 have also been reported in nearly all other human 3D foot kinematics studies (see Rankine et al., 2008). Lundgren et al.'s (2008) bone pin-based study reveals some of the specific joints at which these motions occur: on the lateral side of the foot, plantarflexion and adduction¹ motions are much more pronounced at the cuboid-fifth metatarsal joint than at the calcaneocuboid joint, whereas on the medial side of the foot these motions are more pronounced at the talonavicular joint than at the navicular-medial cuneiform or medial cuneiform-first metatarsal joints. Thus, the joints that contribute most to midfoot mobility during DS2 in humans among those measured by Lundgren et al. (2008) are the talonavicular and cuboid-fifth metatarsal joints, making them relevant targets for comparative morphological analyses.

4.2. Evolution of the longitudinal arch of the foot

Based on the differences in midfoot kinematics between humans and chimpanzees revealed by this study, as well as the possible links between kinematics and joint morphology in humans, we can turn to the hominin fossil record to look for evidence of the evolution of a longitudinal arch. A human-like arch was almost certainly absent from the foot of the 4.4 Ma *Ardipithecus ramidus*, judging from its widely abducted and opposable hallux (Lovejoy et al., 2009). The presence of a human-like hallux is likely critical to longitudinal arch function, as one role of the arch

highlighted in this study is to help position the center of pressure under the medial forefoot and thereby increase the push off leverage of the triceps surae muscles. A mobile hallux, like that of *Ar. ramidus*, would likely be ill-suited to withstand the high joint moments that this would incur. Some have argued for the presence of a longitudinal arch by 3.2 Ma in *Australopithecus afarensis* based on features such as fourth metatarsal torsion (Ward et al., 2011; but see Drapeau and Harmon, 2013) and joint articular surface orientation (DeSilva and Throckmorton, 2010; Prang, 2015), but others have pointed to the possession of a robust navicular tuberosity as evidence that *Au. afarensis* was supporting weight with its medial midfoot and thus lacked a medial arch (Sarmiento and Marcus, 2000; Harcourt-Smith and Aiello, 2004; but see; Prang, 2016a). However, the position and mobility of the hallux of *Au. afarensis* remains highly contentious (Latimer and Lovejoy, 1990; Berillon, 1999; Proctor, 2010; Crompton et al., 2012; Gill et al., 2015; Bennett et al., 2016), and as just discussed, this feature is of considerable importance to reconstructing the presence and function of a longitudinal arch in early hominins. In this study, we also demonstrated that talonavicular and cuboid-metatarsal joint mobility play a critical role in the motion of the human midfoot during push off. *Australopithecus afarensis* possessed human-like cuboid-metatarsal joints (DeSilva, 2010; Ward et al., 2011; Proctor, 2013), but its talonavicular joint morphology is somewhat more ambiguous, with different features indicating a mixed affinity to humans and chimpanzees (Langdon et al., 1991; Sarmiento and Marcus, 2000; Prang, 2016a, b). Given the mixed nature of the evidence, we believe that a definitive diagnosis for the presence of a human-like arch in *Au. afarensis* is still premature, although the presence of some form of intermediate midfoot anatomy is also a possibility.

More concrete evidence for the evolution of a longitudinal arch appears with the genus *Homo*. The 1.8 Ma OH 8 foot specimen, most commonly attributed to *Homo habilis* (Harcourt-Smith and Aiello, 2004), exhibits a suite of features that are indicative of an arch, including a robust, fully adducted hallux (e.g., Day and Napier, 1964; Susman and Stern, 1982) and modern human-like talonavicular and cuboid-metatarsal joints (Sarmiento and Marcus, 2000; DeSilva, 2010; Proctor, 2013; Prang, 2016a, b). The 1.8 Ma fossil metatarsals from Dmanisi that are attributed to *Homo erectus* also include a robust, fully adducted hallux, and present a human-like torsion pattern that is indicative of the presence of an arched foot (Pontzer et al., 2010). Finally, the 1.5 Ma Fwjj footprints from Ileret, also attributed to *H. erectus*, show evidence of an adducted hallux and a narrow instep that is characteristic of a medial longitudinal arch (Bennett et al., 2009). Thus, it is likely that human-like arch function was present in the feet of our ancestors by at least 1.8 Ma. The evolution of a longitudinal arch would have complemented a number of other postcranial adaptations that appeared around this time to help confer more efficient forms of bipedal walking and running (Aiello and Dean, 1990; Bramble and Lieberman, 2004).

5. Conclusions

Although it has long been thought that the evolution of a longitudinal arch reduced midfoot mobility in humans relative to that in other hominoids, the results of this study reveal that the function of the arch during walking is more complex. While human feet are potentially stiffer than those of chimpanzees following heel lift, humans actually use a greater amount of midfoot motion than chimpanzees over the full duration of stance phase. This difference in mobility is driven by motion during the second double-limb support period, when the human midfoot joints are strongly plantarflexed and adducted to assist in push off. Previous comparative studies of hominoid midfoot motion have focused on

¹ Lundgren et al. (2008) present transverse plane motion as movement of the proximal segment relative to the distal segment, thus 'abduction' in their study is equivalent to 'adduction' in this study (C. Nester, pers. comm.).

single-limb support, where chimpanzees use greater midfoot dorsiflexion than humans, resulting in a visible midtarsal break. However, the absolute magnitude of the difference in this motion between humans and chimpanzees during bipedal walking is relatively small (4°), suggesting that the latter are capable of walking with less mobile midfeet than previously appreciated. Based on these findings, we caution against interpreting midfoot joint morphology strictly in terms of range of motion allowed, and instead encourage future studies to consider the ways in which human foot morphology reflects longitudinal arch function throughout the full duration of stance phase, especially at the end of push off.

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Supplementary Online Material

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